# THE LATITUDINAL COMPENSATION HYPOTHESIS: GROWTH DATA AND A MODEL OF LATITUDINAL GROWTH DIFFERENTIATION BASED UPON ENERGY BUDGETS. II. INTRASPECIFIC COMPARISONS BETWEEN SUBSPECIES OF *OPHRYOTROCHA PUERILIS* (POLYCHAETA: DORVILLEIDAE)

JEFFREY S. LEVINTON AND ROSEMARY K. MONAHAN

*Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794*

## ABSTRACT

Individuals of two subspecies of *Ophryotrocha puerilis* (Polychaeta; Dorvilleidae) were collected from differing thermal regimes, and cultures were maintained for over a year. Despite common rearing, the two subspecies show substantial differences in somatic growth rate. At 15°C, the warm-water subspecies grew more slowly, while at 20°C growth for the two subspecies was not significantly different. At 24°C, the warm-water subspecies grew more rapidly and suffered substantially less mortality than the northern subspecies. These results conform to a model predicting genetic differentiation of metabolic efficiency, leading to differences in growth efficiency among populations adapting to thermally differentiated habitats. The problems faced by the cold-water subspecies at 24°C conforms to expectations based upon natural habitat temperatures.

## INTRODUCTION

Many broadly distributed coastal marine species live in a strong thermal gradient and would be expected to be subjected to natural selection to maximize growth efficiency in the local thermal regime. If populations are sufficiently isolated, this may result in a series of genetically distinct subpopulations whose growth characteristics would differ even if reared under constant temperature conditions. In the first paper of this series, Levinton (1983) suggested that a simple model of metabolic expenditure and food (energy) intake would predict divergent temperature optima for subpopulations living under different thermal regimes. Differences among sibling species of the polychaete genus *Ophryotrocha* conform to such a model.

Here we show similar growth differences between two geographically separated subspecies. We compare somatic growth rates of Atlantic and Mediterranean subspecies of *O. puerilis* and show that, despite common rearing through several generations under identical conditions, strong differences in growth rate persist between the two populations. The differences, moreover, show an advantage that shifts from favoring the high latitude population at low temperature, to favoring the low latitude population at higher temperature. These results suggest that the thermal regime generates strong genetic differentiation along the latitudinal gradient. Our results provide more direct evidence of intraspecific latitudinal differences in temperature adaptation than do recorded differentiation in, for example, allozyme polymorphisms (*e.g.,* Levinton and Suchanek, 1978).

*The organism*

*Ophryotrocha puerilis* is a dorvilleid polychaete commonly collected in barely subtidal and intertidal fouling communities in European waters. The species is a protandrous hermaphrodite (sex reversal—from male to female), and occurs as two subspecies, *O. p. puerilis* from Mediterranean waters and *O. p. siberti* from the Atlantic coast of Europe (*e.g.,* Bacci and LaGreca 1953). The two subspecies are reproductively isolated to a variable degree, depending upon the nature of the cross, but incompatibility is generally extensive (Akesson, 1975; 1977). Body size (estimated by number of setigerous segments) at time of sex change differs between the subspecies. Although size at sex change depends somewhat on temperature, *O. p. puerilis* switches at approximately 18 setigerous segments (setigers) while *O. p. siberti* changes at 20 setigers (Bacci and LaGreca, 1953; Sella, 1978). The body length at which sex change occurs is determined by a polygenic system, and selection experiments can change the size at reversal in only a few generations (Bacci and Bortesi, 1961; Sella, 1980).

We used two populations collected by Dr. Gabriella Sella of the University of Torino. The *O. p. siberti* stock was collected in 1978 at the Roscoff Marine station (Brittany, north coast of France), while the *O. p. puerilis* culture was collected in the harbor of Genoa, Italy in 1981. At Roscoff, the annual temperature range is 8.9–15°C: the range is 12.5–24.2°C in Genoa (Sella, 1978). All stocks were kept at room temperature (*ca.* 20°C) prior to being shipped to our laboratory in late 1981. We kept the stocks at *ca.* 20°C until the summer of 1982 when the experiments were performed; both stocks therefore existed for quite a long time under similar conditions. A newborn individual worm becomes a female within about three weeks at 20°C; therefore both stocks went through a number of generations in the laboratory. We doubt that any field conditioning such as local acclimation to temperature could have exerted effects on laboratory stocks over such a long period of time.

## MATERIALS AND METHODS

A number of mating pairs were established for each subspecies by randomly selecting individuals (consubspecifics) and placing pairs in individual glass bowls provided with 30‰ sterilized sea water and ground spinach as food (see Akesson, 1970 for instructions on the culture of *Ophryotrocha*). All mating pairs of each subspecies were kept in an incubator at 20°C, on a 12:12 light/dark cycle. Pairs were then monitored for egg case production. Juveniles of both subspecies hatched out of egg cases after approximately 11 days at 20°C.

Progeny of five pairs of *O. p. siberti* and of four pairs of *O. p. puerilis* were chosen for use in the experiment. On the day that most of the juveniles left each loose jelly egg mass, 48 from each family were isolated in individual glass bowls (30‰ sea water, spinach for food). These bowls were then placed inside plastic boxes (with distilled water on the bottom to slow evaporation). Of these 48 sibs per family, twelve progeny each were moved into incubators at 15, 20, 24, and 28°C. This design placed members of the same family under different temperature conditions, allowing an estimate of among-family difference effects that might persist despite transfer to different temperatures. The design also helps minimize the contribution of among-family differences in confounding an estimate of between-subspecies differences. If completely different families are placed in each and all dishes, then the among-family variance in growth rate cannot be distinguished from a "bowl" effect that happens to make a given family grow faster or slower, due to individual laboratory conditions. This is a problem with the sibling species data presented in Levinton (1983).

The size (number of setigers) of the progeny was then measured every seven days for four time periods. All hatched with zero setigers. Within the first week, all worms of both subspecies kept at 28°C died so this part of the experiment was abandoned. Water was changed when the worms were 21 days past hatching; food was replenished every 7 days if needed (spinach was always provided in excess).

## RESULTS

Figure 1 summarizes the results for all families of *O. p. siberti* (northern subspecies) and *O. p. puerilis*. A decided shift in somatic growth rate occurs from low to high temperature. At 15°C, the northern subspecies grows most rapidly, while at 20°C growth rate is fairly similar for the two subspecies. At 24°C, however, the northern
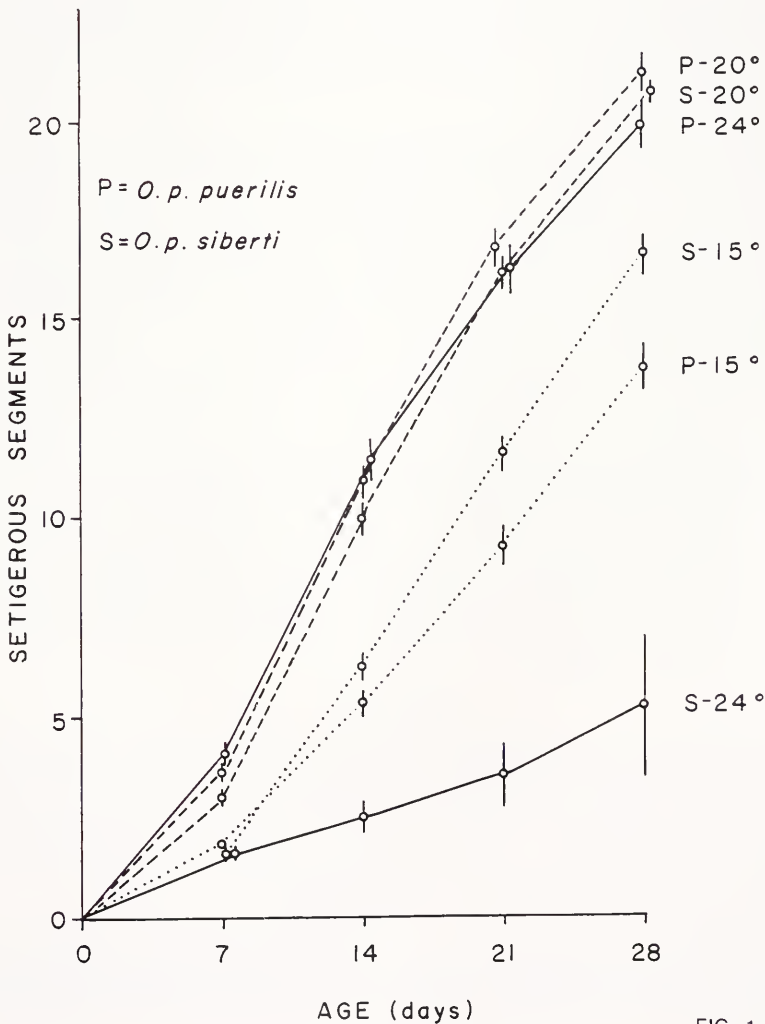


FIGURE 1. Summary of growth data (means ± 95% confidence) for individuals of all families of the two subspecies.

subspecies grows very slowly while the southern subspecies grows much more rapidly. The growth of the southern subspecies is less at 24°C than at 20°C. This indicates that even the southern subspecies is nearing its upper thermal limit at 24°C.

Growth plots for individual families show the pattern of growth differences between the two subspecies (Fig. 2). At 15°C the growth of families from the southern subspecies is less than that of the northern subspecies, with some overlap (Nested ANOVA, $F = 6.88$, $P < .05$). At 20°C the families from both subspecies overlap substantially ($F = 0.42$, Difference not significant). At 24°C, however, growth of the northern subspecies is clearly depressed relative to the southern subspecies ($F = 59.69$, $P < .001$).

The northern subspecies thus displays a growth disadvantage at higher temperature. This disadvantage is also reflected in a noticeable incidence of setiger resorption and generally poor nutritive condition. Not surprisingly, mortality in the experiment at 24°C was greater for *O. p. siberti* than for *O. p. puerilis* (Fig. 3). Most individuals that survived grew poorly; a few, however, grew at rates rather similar to those of the Mediterranean subspecies. This may represent genetic variation for the trait, but we have not followed this up.

Although there are clear intersubspecific differences, we wondered if there were significant among-family differences in growth rate, as reported in Levinton (1983). To test for this we performed a three-way analysis of variance, using temperature, family, and time as the variables. Since we had used the same families from a given subspecies in all of the temperature treatments we could estimate whether the use of different families caused an additional variance component. Table I shows the results for both subspecies. In both cases significant among-family differences in growth rate can be found when time and temperature are factored out.

In a sense, this analysis is problematical because the body size of a given individual at a given time is not independent of the previous time. Thus the relative magnitude of a family mean size may persist for more than one time period. To eliminate the problem, we performed two-way analyses of variance at a given time, using temperature and family as the variables. Table II shows the results for seven days and for 28 days. At seven days, significant and persistent among-family differences in growth occur despite rearing in several temperatures. At 28 days, however, no significant additional variance component is generated by family difference. This change may represent initial family differences that were eliminated subsequently by acclimation to new common conditions over the course of the experiment, and, possibly, mortality of more slowly-growing worms.

## DISCUSSION

Our results demonstrate a shifting growth advantage consistent with the differing thermal regimes of the two subspecies. They conform to an hypothesis which predicts that local evolution should maximize metabolic efficiency and thus favor maximum growth under local thermal conditions (Levinton, 1983). Thus, despite common rearing for several generations under common conditions, the evolved differences between the populations emerge as growth differences.

The latitudinal compensation hypothesis weighs heavily on the interpretation of life-history differences among natural populations of a given species living along a thermal (*e.g.*, latitudinal) gradient. In any study of growth, body size, and age of first reproduction, temperature may have to be considered as a primary influence on life-history traits.

Although traditional studies of latitudinal differentiation in growth and metabolism accounted for such a limitation (*e.g.*, Weymouth and McMillan, 1931; Rao, 1953;
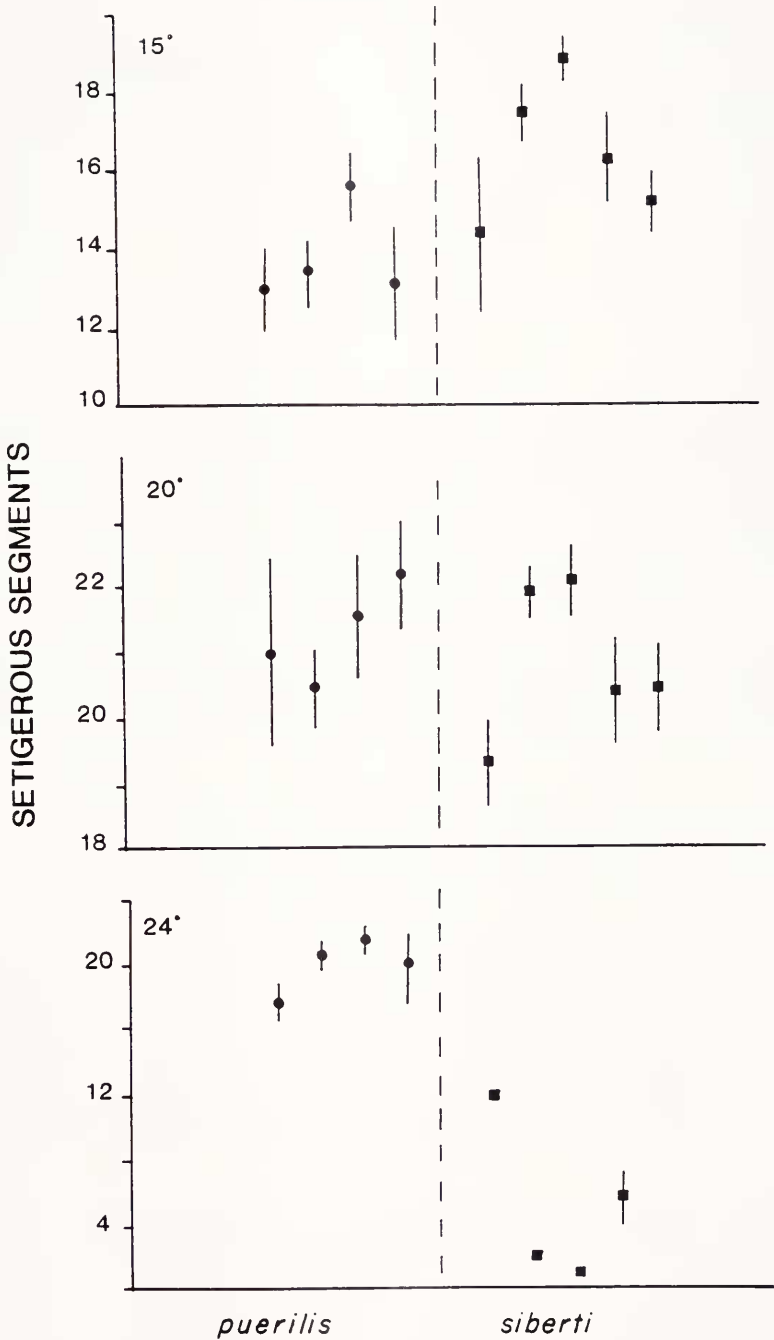
FIGURE 2.  Mean individual growth (number of setigerous segments after 28 days), ±95% confidence, among the families of *Ophryotrocha puerilis puerilis* and *O. p. siberti* at 15, 20, and 24°C.
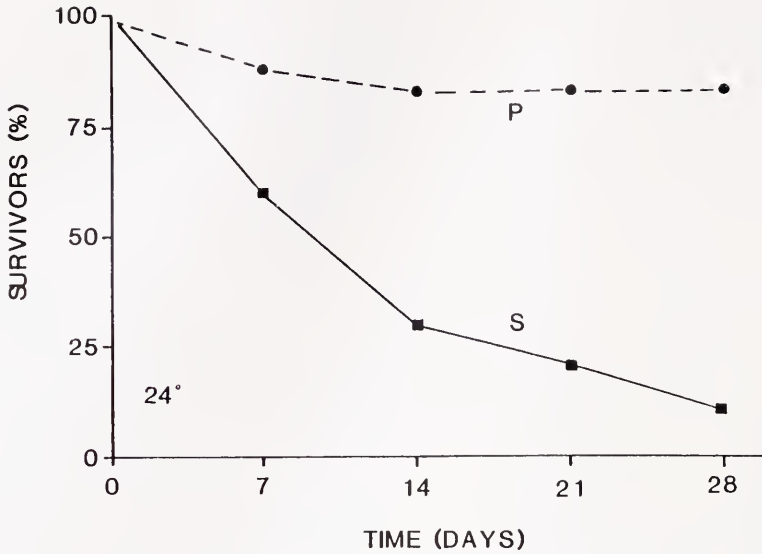
FIGURE 3.  Survival of individuals of the two subspecies at 24°C.

Vernberg and Vernberg, 1966, among others), recent workers have tended to assume that latitudinal differences in life history patterns reflect differences in demography which, in turn, select for different ages of first reproduction, investment in growth

TABLE 1

*Three-way analysis of variance for the growth experiment, testing for differences among families, temperatures, and sampling times*

*Ophryotrocha puerilis puerilis:*

| Source of Variation | DF | SS | MS | F |
|---|---|---|---|---|
| Temperature (T) | 2 | 318.74 | 159.37 | 651.79*** |
| Families (F) | 3 | 42.29 | 14.10 | 57.64*** |
| Sampling Week (W) | 3 | 1544.02 | 514.67 | 2104.86*** |
| T × F Interaction | 6 | 15.02 | 2.50 | 10.24*** |
| T × W Interaction | 6 | 47.59 | 7.93 | 32.44*** |
| F × W Interaction | 9 | 5.51 | 0.61 | 2.51 |
| T × F × W Interaction | 18 | 4.40 | 0.25 | |

*Ophryotrocha puerilis siberti:*

| Source of Variation | DF | SS | MS | F |
|---|---|---|---|---|
| Temperature (T) | 1 | 129.67 | 129.67 | 474.12*** |
| Families (F) | 4 | 53.01 | 13.25 | 48.45*** |
| Sampling Week (W) | 3 | 1510.14 | 503.38 | 1840.52*** |
| T × F Interaction | 4 | 1.00 | 0.25 | 0.91 |
| T × W Interaction | 3 | 16.22 | 5.41 | 19.77*** |
| F × W Interaction | 12 | 4.63 | 0.39 | 1.41 |
| T × F × W Interaction | 12 | 3.28 | 0.27 | |

*** $P < .001$.
Data for *Ophryotrocha puerilis siberti* exclude 24°C, due to low sample sizes.

TABLE II

*Two-way analyses of variance considering variation in growth among temperatures and families at 7 and 28 days*

| Subspecies | Time (days) | Family | | Temperatures | |
|---|---|---|---|---|---|
| | | F | P | F | P |
| O. p. puerilis | 7 | 5.52 | <.05 | 15.71 | <.01 |
| O. p. puerilis | 28 | 2.84 | NS | 69.74 | <.01 |
| O. p. siberti | 7 | 11.57 | <.01 | 17.42 | <.01 |
| O. p. siberti | 28 | 0.37 | NS | 31.28 | <.01 |

NS: Not Significant ($P > .05$).

*versus* reproduction. In a study of the turban snail *Tegula funebralis*, Frank (1975) concluded that the smaller reproductive size of individuals in low-latitude habitats resulted from increased adult mortality relative to high latitudes. Such an interpretation has also been used by Boehlert and Kappenman (1980) to explain latitudinal patterns in size at reproductive maturity in a fish species. While adult mortality clearly can influence life history tactics (Stearns, 1976; Charnov, 1981), one cannot safely interpret latitudinal patterns of life history change as being due to demography alone. Our results and Levinton's (1983) model clearly show that temperature can strongly influence latitudinal variation in growth.

Some recent studies support the role of temperature in latitudinal patterns in life-history tactics. For example, Searcy (1980) shows that latitudinal body size clines in birds are best explained as an adaptation to conserve body heat. Birds living above a certain temperature need not consume energy to cool the body. Below a certain temperature for a given body volume, however, the rate of heat loss is not matched by the rate of heat production of a bird that is "thermally neutral," *i.e.*, producing enough heat to maintain typical passerine body temperature. An increase in body volume tends to reduce the rate of heat loss and therefore permits a bird to survive lower temperatures with no additional metabolic cost.

Levinton and Lonsdale (1983) have examined latitudinal patterns of growth and body size in the harpacticoid copepod *Scottolana canadensis* taken from localities from Maine to Florida. They reared populations under common conditions through several generations, and found strong differences in growth rate. These differences reflected a growth advantage of high latitude derived populations at low temperatures and the reverse at high temperature. Body size of northern-derived populations also was larger than southern-derived individuals at all temperatures despite common rearing. They suggest that both growth and body size are controlled by thermal constraints.

Several studies of latitudinal differences in growth rates have explained the acceleration of growth of high latitude (or altitude) populations, relative to low latitude (altitude) populations at low temperatures as being a form of compensation (Ament, 1979; Bervan *et al.*, 1979). The higher altitude forms grow more rapidly to compensate for the effect of lowered temperature on poikilothermic activities. Clarke (1982) suggests that slow growth in arctic forms reflects a strategy to deal with chronically low food availability.

We might speculate that the difference in size of the male-female switch in sex between subspecies may also reflect thermal limitations. The size of sex switch should be determined by the relative fecundities of males and females as a function of

increasing size. Consider the case where temperature increases. Although temperature increases metabolic demand, it also increases activity and, therefore, the rate of feeding. As long as the animal is not near its upper thermal limit the energy gain in feeding will increase disproportionately, relative to increased metabolic demand. Increasing temperature will thus increase female fecundity for a given body size. If sperm are energetically cheap to produce then there may be no difference in male fecundity with differing temperature. Increasing temperature, therefore, will increase female fecundity, relative to that of the male, at a given body size. This is sufficient to cause evolution of a decreased size of male to female switch as a response to increased temperature. Our prediction is complicated, however, by the ability of individuals of this species to undergo repeated sex changes following the initial size-specific switch. These secondary sex changes can be provoked by interactions among worms and nutritional condition (Pfannenstiel, 1975, 1977; Berruti, 1980).

We conclude that the effects of temperature probably affect all life history features of a poikilothermic organism. It therefore will be important in future studies to account for temperature in studies of life histories, along with such factors as stochastic processes of population extinction, mortality schedules, and other factors known to govern the evolution of growth and reproductive strategies.

## ACKNOWLEDGMENTS

## LITERATURE CITED

AKESSON, B. 1970. *Ophryotrocha labronica* as a test animal for the study of marine pollution. *Helgol. wiss. Meeresunters.* **20**: 293–303.

AKESSON, B. 1975. Reproduction in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *Publ. Staz. Zool. Napoli* **39**(suppl.): 377–398.

AKESSON, B. 1977. Crossbreeding and geographic races: experiments with the polychaete genus *Ophryotrocha. Mikrofauna Meeresboden* **61**: 11–18.

AMENT, A. 1979. Geographic variation in relation to life history in three species of the marine gastropod genus *Crepidula:* growth rates of newly hatched larvae and juveniles. Pp. 61–76 in *Reproductive Ecology of Marine Invertebrates,* S. E. Stancyk, ed. Univ. South Carolina Press, Columbia, SC.

BACCI, G., AND O. BORTESI. 1961. Existence of multiple sex genotypes in the hermaphrodite polychaete worm *Ophryotrocha puerilis siberti. Nature* **190**: 838.

BACCI, G., AND M. LAGRECA. 1953. Genetic and morphological evidence for subspecific differences between Naples and Plymouth populations of *Ophryotrocha puerilis. Nature* **171**: 1115.

BERRUTI, G. 1980. The effect of starvation on the appearance of the definitive upper jaw in *Ophryotrocha puerilis* (Annelida, Polychaeta). *Boll. Zool.* **47**: 71–74.

BERVAN, K. A., D. E. GILL, AND S. J. SMITH-GILL. 1979. Countergradient selection in the green frog, *Rana clamitans. Evolution* **33**: 609–623.

BOEHLERT, G. W., AND R. F. KAPPENMAN. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the Northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* **3**: 1–10.

CHARNOV, E. L. 1981. Sex reversal in *Pandalus borealis:* effect of a shrimp fishery. *Mar. Biol. Lett.* **2**: 53–57.

CLARKE, A. 1982. Temperature and embryonic development in polar marine invertebrates. *Int. J. Invert. Reprod.* **5**: 71–82.

FRANK, P. W. 1975. Latitudinal variation in the life history features of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). *Mar. Biol.* **31**: 181–192.

LEVINTON, J. S. 1983. The latitudinal compensation hypothesis: Growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta: Dorvilleidae). *Biol. Bull.* **165**: 686–698.

LEVINTON, J. S., AND D. J. LONSDALE. 1983. Latitudinal differentiation in copepod growth: physiological and evolutionary significance. *Proc. Nat. Acad. USA,* submitted.

LEVINTON, J. S., AND T. H. SUCHANEK. 1978. Geographic differentiation, niche breadth, and genetic differentiation at different geographic scales in the mussels, *Mytilus californianus* and *M. edulis. Mar. Biol.* **49:** 363–375.

PFANNENSTIEL, H.-D. 1975. Mutual influence on the sexual differentiation in the protandric polychaete *Ophryotrocha puerilis.* Pp. 48–56 in *Intersexuality in the Animal Kingdom,* R. Reinboth, ed. Springer-Verlag, Heidelberg.

PFANNENSTIEL, H.-D. 1977. Experimental analysis of the 'Paarkultureffekt' in the protandric polychaete, *Ophryotrocha puerilis* Clap. Mecz. *J. Exp. Mar. Biol. Ecol.* **28:** 31–40.

RAO, K. P. 1953. Rate of water propulsion in *Mytilus californianus* as a function of latitude. *Biol. Bull.* **104:** 171–181.

SEARCY, W. T. 1980. Optimum body sizes at different ambient temperatures: an energetics explanation of Bergmann's rule. *J. Theor. Biol.* **83:** 579–583.

SELLA, G. 1978. Responses adaptatives a differentes temperatures chez les deux sous-especes d'*Ophryotrocha puerilis* (Claparede et Mecznikow), au cours de la phase male. *Cah. Biol. Mar.* **19:** 117–125.

SELLA, G. 1980. The genetic system controlling the body length at which sex change occurs in *Ophryotrocha puerilis* (Annelida, Polychaeta). *Atti. Soc. Toscana Sci. Nat. P. V. Mem. Ser. B* **87:** 197–203.

STEARNS, S. C. 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol.* **51:** 3–47.

VERNBERG, W. B., AND F. J. VERNBERG. 1966. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca.* V. Effect of temperature on tissue respiration. *Comp. Biochem. Physiol.* **17:** 118–126.

WEYMOUTH, F. W., AND H. C. MCMILLAN. 1931. The relative growth and mortality of the Pacific razor clam (*Siliqua patula* Dixon) and their bearing on the commercial fishery. *Bull. U. S. Bur. Fish.* **46:** 543–567.